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## THE MOSAIC OF SINGLE AND TWIN CONES IN THE RETINA OF FISHES.<sup>1</sup>

CARL H. EIGENMANN AND GEORGE DANIEL SHAFER.

THE eyes of fishes have served as the basis of numerous papers. A list of these dealing with the eye in its macroscopic aspect has been furnished by Ziegenhagen ('95), while those dealing with its minute structure have been enumerated by Krause ('86) and Cajal ('94).

During recent years the efforts have been largely in the direction of the application of the methods of Golgi and Ehrlich, chiefly to work out the vertical relationships of the various layers of the retina. The present paper will be devoted to the horizontal relationships of two elements in the retina of fishes, *i.e.*, the single and the twin cones.

Both elements are well known, and their relative positions have also received mention, as will be seen from the following summary of the literature.

The twin cones arise from two cells placed close together; their nuclei are usually just within the outer limiting membrane. The cone bodies are pressed together so that the faces in contact are flat. The outer segments are separate. The line joining the centers of the two elements of the twin cone may be termed the axis of a twin. The single cones vary greatly in their relative thickness when compared with the components of a twin. Quite frequently they are much thinner than the latter, and in some other instances their structure is strikingly different. In the eye of *Zygonectes*, for instance (Eigenmann ('99)), the basal portion of the single cones contains refractive granules, increasing in size outward where the series ends in a lenticular vacuolated body separating the granular from the distal portion. The twins do not possess these granules. In

<sup>1</sup> *Contributions from the Zoölogical Laboratory of the Indiana University, No. 26.*

Coregonus the outer segments of the single cones have a central deeper staining core. In this respect they agree with the rods. One of us was in doubt concerning these single cones, inclining to the opinion that they were rods (Eigenmann ('99), p. 548).

The rods are not taken into consideration in this paper. It may be said, however, that generally the number of rods is inversely proportional to the number of single cones.

The eyes examined were taken, for the most part, from museum specimens preserved in alcohol, and originally not intended for anatomical or histological purposes. The eyes were sectioned in paraffine, and the sections stained with hæmalum and eosine, or the Biondi-Ehrlich three-color mixture, or Weigert's hæmatoxylin; the latter gave good results even with the alcoholic material. No attempt has been made in this paper to describe the extent of variation in the patterns noted in different parts of the same retina.

The earliest notice that may have a possible bearing on the present subject is that of Guennelon (1686). According to Ziegenhagen, he noted that the retina of *Gadus æglifinus* is striped. We are not at all sure that this observation related to the arrangement of the twin and single cones.

The first undoubted notice that the twin and single cones may form a definite pattern was that of Hannover ('43), who figured the pattern of the "Rödspetten" and of the pike. Both patterns figured are those of our diagram *D*. We find the pattern of the pickerel to be that of diagram *H*.

Much later, Müller ('72, p. 59) says that in *Perca fluviatilis* the twins are in excess, with such an arrangement that each single cone is separated from its neighbor by the twins, not counting the rods. He also stated that in many fishes only single cones exist.

Nunneley ('58) and Krause ('68) described cones in the eel, and here, according to Krause, only single cones are found.

Friis ('79) examined a large series of fishes and found that in *Accipenser* and *Anguilla* only single cones exist. He found twin cones only in a large number of species, but states that in all of these, single cones are always to be found about the *ora*

*serrata*. Among the species that he enumerates as possessing twin cones only, there are certainly some in which single cones are regularly distributed. He found twin cones only in the retina of Scomber, Thynnus, Mugil, Gadus, Platessa, Hippoglossus, Rhombus, *Salmo trutta*, Coregonus, *Clupea harengus*, and *Clupea sprattus*.

He found both twin and single cones in *Belone rostrata*, Tinca, Ammodytes, Carassius, Abramis, Leuciscus. In the selachians examined, only rods are to be found.

Ryder ('95) discovered a regularity of arrangement of rods and cones in the larva of *Salmo salar*. The rods referred to are the single cones of authors. He believed this definite grouping of rods and cones to have some homology with the compound eye of the invertebrate. The arrangement he found is that of our pattern *D*.

Beer ('98) in a footnote calls attention to the fact that the cone mosaic is surprisingly plain and regular in *Scorpæna* and *Blennius*, and can be seen with the ophthalmoscope. He figures pattern *F*.

Eigenmann ('99) calls attention to the regularity of arrangement in *Zygonectes*. The pattern noted is *E*, a slight modification of that noted by Ryder in *Salmo*. He also found that in *Chologaster* the twins predominate over the single cones, and that in this genus the arrangement of the twins is a modification of pattern *C*.

Finally Eigenmann and Hansell ('99) in a short abstract state that the twin and single cones are arranged in a regular pattern, and that this pattern is either that described by Hannover and by Ryder for fishes, or a slight modification of this pattern.

The first notice of a regular alternation of twin and single cones is that by Hannover, and of the arrangement of twin and single cones, with a definite arrangement of the axes of the twin cones, is that by Ryder.

The work begun by Mr. G. Hansell under my direction has been continued by Mr. Shafer and myself, and a number of species have been examined to date. Mr. Hansell's work is incorporated in the present paper, credit being given under the

head of the species he examined. We have found that the arrangement of the twin and single cones is remarkably constant for any given species,<sup>1</sup> and that the arrangement differs considerably in different groups of fishes, but that the patterns in all of the species examined can be derived seriatim from one or the other of the patterns.

Pattern *A*, the pattern from which all others can most readily be derived, has not been found in any species as yet, but slight modifications of it have. In this simple pattern there are twin cones only, and the axes of alternate rows of twins are parallel, while those of neighboring rows are at right angles to each other. A series of squares are formed in this way whose sides are the extended axes of four twin cones.

Pattern *B* is produced by a slight twisting of the axes of the twins so that if extended they would form a rhomb. This pattern was found in

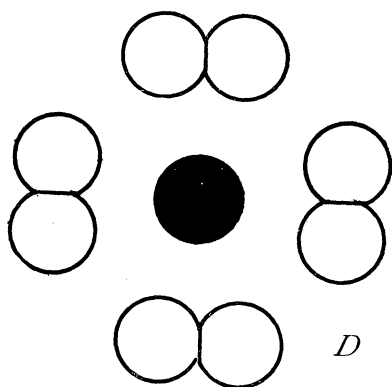
*Scorpena porcus*. The angles of the rhomb measure  $53^\circ$  and  $127^\circ$ . The actual conditions found in the eye are shown in Fig. 1.

Pattern *C* is produced from *B* by a still further twisting of the axes of the twins till they are parallel

<sup>1</sup> The variation of the pattern in different parts of the same eye will be dealt with in a later paper.

to each other. This pattern was found in *Sebastodes elongatus* (Fig. 2). A similar but less regular arrangement was found by Eigenmann ('99) in *Chologaster cornutus* (Figs. 3, 4<sup>2</sup>). In the latter case there are also some single cones irregularly disposed among the twins.

Pattern *D* is formed from *A* by the addition of a single cone in the center of the square. This pattern has been known longer than any other, and is evidently the one described by Müller for *Perca*, in which he says "each single cone is separated from its neighbor by twins." It is found in the American and

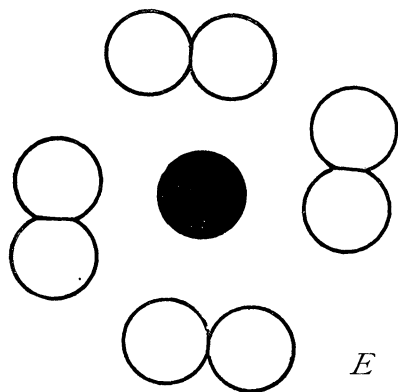


the European species of *Perca* (Fig. 5), in which the single cones are of nearly the same size as the components of the twins, and in *Micropterus* (Fig. 9). It was also found in *Etheostoma caeruleum* (Fig. 6), *Apomotis cyanellus* (Fig. 7), and *Pimephales notatus* (Fig. 8). The three last eyes were pre-

pared and the figures drawn by Mr. Hansell.

The closeness of the elements in the pattern and the size of the elements are seen to differ in the various species examined.

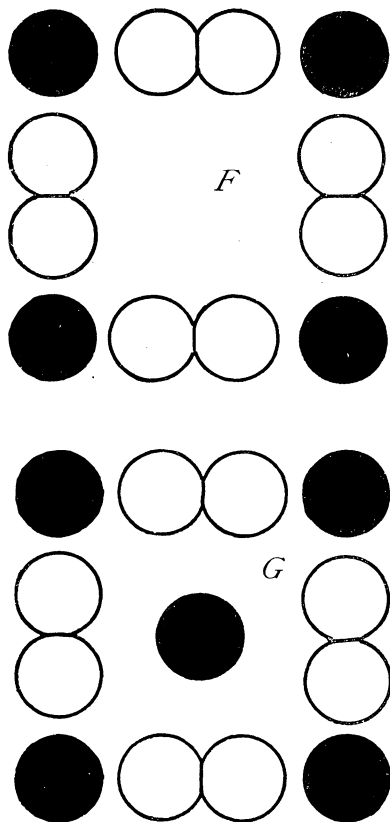
Pattern *E* is but a slight modification of pattern *D*, in which some of the twins have migrated along the faces of the squares so that while their



axes, if extended, still form squares, the lines separating the twins, if extended, form parallel lines instead of a continuous line. This condition was found by Eigenmann ('99) in *Zygonectes* (Figs. 10, 11).

Pattern *F* is formed by adding a single cone at each angle

of the square of pattern *A*. This gives us rows which answer to the description of Müller quoted above, but this pattern evi-

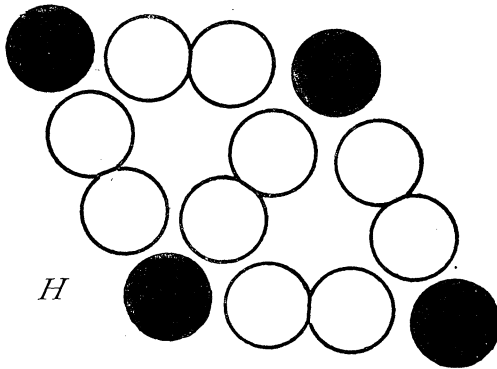


dently was not the one observed by him. This pattern was first figured by Beer ('98) in *Blennius*, in which the large hollow square formed is filled by a great number of rods. The actual pattern found in the eye of *Blennius* was of interest (Fig. 12), inasmuch as double series of twin cones, one with axes horizontal and one with axes vertical, were, in several places, interpolated without disturbing the pattern already present.

Pattern *G* is formed by adding a single cone in the center of the hollow square of pattern *F*. This pattern was described by Ryder ('95) in *Salmo*. A pattern but a little less regular was found in some larval *Coregonus* (Figs. 13-17).<sup>1</sup>

<sup>1</sup> Inasmuch as these specimens of *Coregonus* were of interest in several respects, a brief note may be added to the above. The material examined consisted of recently hatched larvæ preserved in 70 per cent alcohol. The material came from the hatching station of the U. S. Fish Commission. The heads were imbedded in paraffine, sectioned and stained in hæmalum-eosine or in Biondi-Ehrlich's three-color mixture. Both methods gave excellent results. The twins alternate with the single cones in such a way that each is surrounded by four twins whose dividing plane points toward the space occupied by the single cone. The pattern is not mathematically accurate in the eye. Many of the twin cones are twisted, as it were, on their axes, and occasionally an extra single cone is to be found besides the single one in the unoccupied space between four twin cones, *i.e.*, at the angles of the square. Each component of a twin cone consists of a slender outer segment, a much thicker body, and a more or less vacuolated base

Pattern *H* is the most complicated found so far. The square of pattern *F* is converted into a rhomb with angles of  $60^\circ$  and  $120^\circ$ , and a twin cone is added whose axis forms a diagonal between the nearer angles of the rhomb. This makes two equilateral triangles whose sides are formed by twin cones, and



whose angles are occupied each by a single cone. This pattern has been found in *Lucius* (Figs. 18, 19).

No suggestion is offered as to the significance of these various patterns or the causes that have led to the various modifications.

In several species we have not so far been able to make out any regularity or, in fact, the nature of the cones. These are the catfishes and *Catostomus*, one of the suckers.

resting on the outer limiting membrane (Fig. 1). Below this membrane and exactly opposite each cone is a conical nucleus with a diameter less than that of the cone. With Biondi-Ehrlich the nuclei are stained a blue purple and the rest of the structures pink, so that there is no difficulty in separating parts. The single cones differ from the twins in possessing a central deeper staining core in the outer segment (Fig. 13). Besides these nuclei there are a few others, more spherical and slightly larger, just within the inner ends of this layer of cells — the rod nuclei. This inner layer of cells seems most abundant about midway between the optic nerve and the *ora serrata*. There are about two and one-half times as many of the outer nuclei as of these inner.

## EXPLANATION OF FIGURES.

(Eigenmann, Figs. 1-5 and 10-19; Hansell, Figs. 6-9.)

All the figures were made from paraffine sections by the aid of the *camera lucida*. All but one of the figures were made under a magnification either of the Zeiss apochromatic 2 mm., or the Bausch and Lomb,  $\frac{1}{2}$  objective.

(1) Pigment epithelium; (2) rods and cones; (3) outer nuclear layer; (4) outer reticular layer; (5) horizontal cells; (6) inner nuclear layer; (7) spongioblastic layer; (8) inner reticular layer; (9) ganglionic layer; (10) optic fibre layer; *cu.*, cones; *cu. nl.*, cone nuclei.

FIG. 1. — Arrangement of cones in *Scorpaena porcus*, 2 mm.

FIG. 2. — The same of *Sebastodes elongatus*.

FIG. 3. — Vertical section through the retina of *Chologaster papilliferus*, depigmented with chromic acid and stained with Biondi-Ehrlich's three colors, 2 mm.

FIG. 4. *a, b, c.* — A series of three oblique sections through the retina, 2 mm. (*a*) Passes from the outer margin of the retina to the base of the cone bodies. (*b*) Passes through the basal segments of the cones. (*c*) Passes through the cone nuclei.

FIG. 5. — Arrangement of cones in the retina of Perca,  $\frac{1}{2}$ .

FIG. 6. — The same of *Etheostoma caeruleum*,  $\frac{1}{2}$ .

FIG. 7. — The same of *Apomotis cyanellus*.

FIG. 8. — The same in *Pimephales notatus*.

FIG. 9. — The same in *Micropterus salmoides*,  $\frac{1}{2}$ .

FIG. 10. — Vertical section through the retina of *Zygonectes notatus*, 2 mm.

FIG. 11. — Tangential section of the retina at the depth of the cone bodies, showing the arrangement of the cones, 2 mm. and 6 mm.

FIG. 12. — Arrangement of the cones in *Blennius ocellaris*, 8 mm.

FIGS. 13-16. — Successive tangential sections through the retina of a newly hatched Coregonus. The sections represent the posterior face of successive sections through the same part of the retina, 2 mm.

FIG. 13. — Passes through the outer part of the inner segments of the cones and the inner ends of the pigment cells.

FIG. 14. — Passes through the bodies of the cones and shows to best advantage the arrangement of the cones.

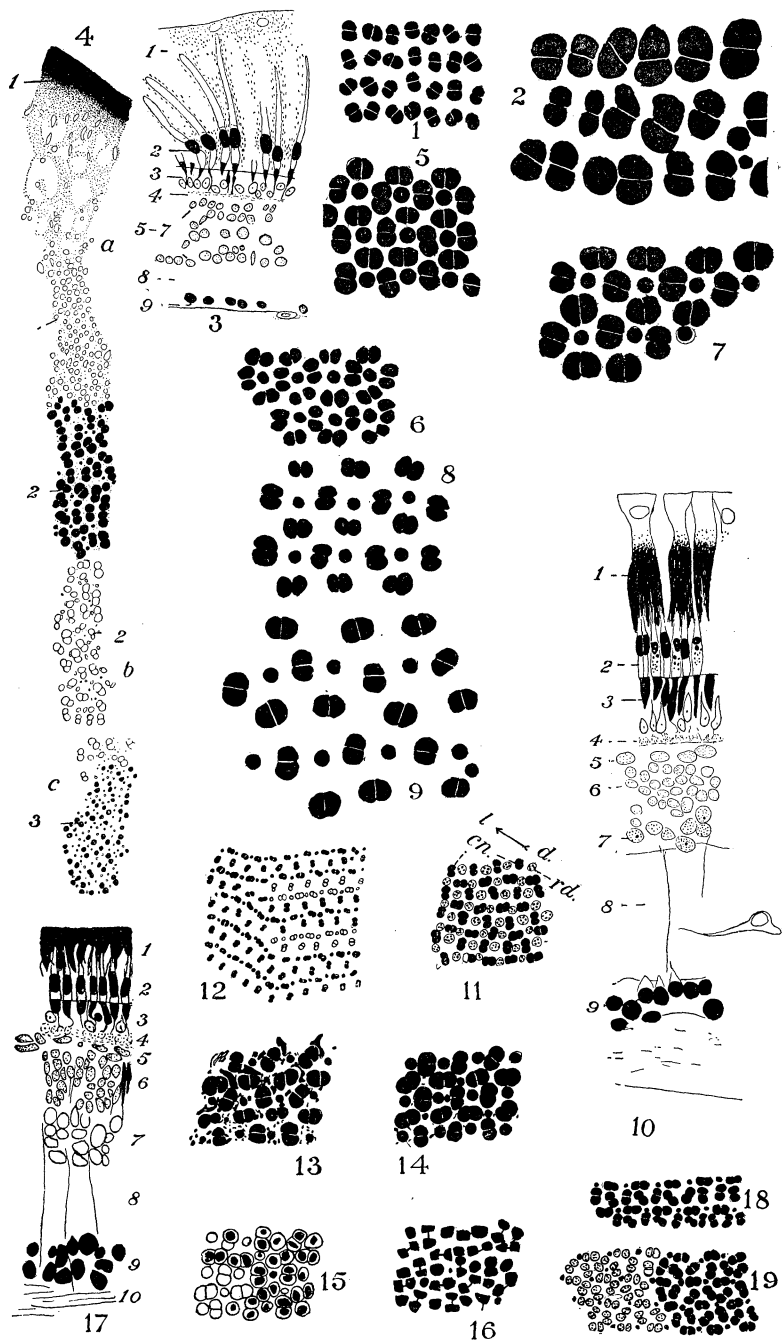
FIG. 15. — Section containing the inner ends of the cones and the outer ends of the nuclei belonging to them.

FIG. 16. — The middle of the cone nuclei.

FIG. 17. — Median section of the retina of a newly hatched *Coregonus* sp. (?), 2 mm.

FIG. 18. — Arrangement of the cones in *Lucius vermiculatus*.

FIG. 19. — Arrangement of the cones and cone cells in *Lucius vermiculatus*, the cones on the right, the cone cells on the left, of the figure, 2 mm.



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